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NOTES ON THE DISTRIBUTION AND ABUNDANCE OF GROUND- AND ARBOREAL-NESTING ANTS (HYMENOPTERA: FORMICIDAE) IN SOME COSTA RICAN CACAO HABITATS

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Abstract.—The number of species and approximate colony sizes including presence/absence of brood were determined from multiple samples of forty arboreal, rotten cacao pods (*Theobroma cacao* L.) for each of seven widely scattered censuses over a two-year period at one locality (Finca La Tigra) in northeastern Costa Rica. Similar data were obtained for a one-year period (three scattered censuses) for experimental plots of various ground substrates (rotting banana trunk slices, cacao pod husks, leaf litter) in two contrasting cacao habitats (well-maintained cacao "plantation" and "cacao forest") at a different locality (Finca Experimental La Lola) within the same climatic region. Although close to 30,000 ants, representing 10 genera and 16 species, were collected from arboreal pods at La Tigra, there was only 25% faunal overlap with the ground-nesting samples from La Lola. *Crematogaster limata palans* Forel was one of a few "dominant" species in arboreal pods at La Tigra, but was entirely absent in the La Lola ground samples. In each habitat, a few species were dominants, in terms of colony size range and the frequency of occupancy of nesting substrates, and the majority of ant species were "rare." Of about 14,000 ants representing 19 genera and 26 species censused at La Lola about 60% occurred in the cacao forest. The plantation habitat had 12 genera and 16 species. There was overlap in ant genera and species between the two La Lola habitats. The slices of rotting banana trunk supported the greatest number of ant species in both habitats.

Co-occurring ant species within a habitat often exhibit definitive patterns of resource partitioning, within and outside of the tropics (e.g. Brian, 1955; Briese, 1982; Briese and Macauley, 1980; Byron et al., 1980; Carroll and Janzen, 1973; Cole, 1983; Jeanne, 1979; Levings, 1983; Levings and Franks, 1982; Melhop and Scott, 1983; Plowman, 1981; Smallwood, 1982; Swain, 1980; Wilson, 1971 and many included references; Young, 1983). Such patterns are known for other insects as well (e.g. Allee et al., 1949; Anderson, 1982; Bahrmann, 1980; Hanski, 1980; Karoji, 1980; Prince and Parsons, 1980; Ranta and Lundberg, 1980; Schmalfuss and Ferrara, 1982). Tropical forests, in particular, are exceedingly rich in ant species (e.g. Ayre, 1977; Evans, 1982; Kempf, 1975; Levings and Franks, 1982; Wilson, 1976a, b). Furthermore, contrasting tropical habitats, such as agricultural plantings and nearby forest, often exhibit pronounced differences in the overall

"species richness" of both ground-nesting and arboreal-nesting ants (e.g. Adams et al., 1981; Banerjee, 1983; Fabres and Brown, 1978; Saks and Carroll, 1980; Samways, 1981, 1983).

The cacao plantation, in particular, both in the New World and Old World tropics, has been contrasted, in terms of its ant fauna, with other habitats (e.g. Evans and Leston, 1971; Jackson, 1984; Leston, 1970, 1973, 1978, 1979; Lieberman and Dock, 1982; Young, 1983). Such studies generally show that tropical forest habitats contain a greater number of ant species than agricultural habitats (e.g. Jeanne, 1979; Leston, 1979; Lieberman and Dock, 1982), although not always (Young, 1983). In this paper I present new data on the distribution and abundance of ant species in contrasting cacao habitats in Costa Rica. Emphasis is placed upon the comparison of ant assemblages associated with a variety of ground substrates as well as that of arboreal, rotten cacao pods within each habitat studied. The data support the contention that abandoned cacao groves, reverting to rain forest, contain a greater species richness of ants than maintained plantations, and that the fauna of arboreal rotten pods is markedly different from that of nearby ground substrates.

Materials and Methods

These studies were conducted at two localities, both within the Caribbean watershed zone of Costa Rica: (1) "Finca La Tigra," near La Virgen (10°23′ latitude, 84°07′ longitude), Sarapiqui District, Heredia Province (220 m elev.); (2) "Finca Experimental La Lola," near Siquirres (10°06′N, 83°30′W) (approx. 50 m elev.), Limon Province. Both localities are within the premontane-to-lowland tropical rain forest region of Costa Rica, and experience a short dry season generally in March–April each year (Figs. 1, 2).

Cacao groves at La Tigra are about 35 years old, whereas those of La Lola and adjacent properties date back into the 1920s. The La Tigra site is adjacent to extensive rain forest, including the recently-established Braulio Carillo National Park. In contrast, most of the surrounding area at La Lola is highly disturbed secondary-growth and plantations in varying stages of abandonment.

Between December 1982 and December 1984, I censused ant colonies in samples of exactly forty arboreal, rotten cacao pods from the same approximately 100 × 100-meter area of cacao at La Tigra. Only soft, blackened pods within the size range of a 6 × 2 cm (smallest) to 15 × 7 cm (largest) were collected from trees of mixed varieties, and within a height range of 1.0 to 2.0 m. Pods were placed in large plastic bags and examined at a nearby field station. Each pod was broken apart and its contents examined for ants and associated organisms. For each pod, the presence or absence of adult and brood were recorded. A voucher sample of each ant species was preserved, with a "morphospecies" description. Whenever possible, brood samples were also collected. An attempt was made to estimate the total size of colonies. I used these figures to determine an estimate of ant "biomass," defined here as the total number of individuals collected at a given census. La Tigra cacao pods were thus examined for ants for a total of seven, widely-scattered census dates, corresponding to "dry" (March), "mid-rainy" (August), and "late rainy" (November) seasons: 1982: 3–4 December; 1983: 2–3 March, 7–8 August, and 10–11 November; 1984: 28–29 February, 3–4 August, and 20 November.

Fig. 1. Monthly rainfall pattern for "Finca La Tigra" in northeastern Costa Rica for the study period (1982–1984). Note dramatic drop in rainfall in March–April each year. The dry season actually begins in mid to late February at this locality. Data courtesy of Dr. J. Robert Hunter, for "Finca La Tirimbina" meteorological station; about 2 km from La Tigra.

At La Lola, I censused ants in ground substrates experimentally distributed in two constrasting cacao ("Matina" variety) habitats: banana trunk slices, cacao pod husks, cacao leaf litter, and for one census (November 1984), arboreal, rotten cacao pods. Ant populations of a well-maintained cacao plantation ("Section 25") of the La Lola farm were contrasted with those of an adjacent, abandoned cacao plantation belonging to Amos Barker. The Barker cacao resembles a forest, and I call it the "cacao forest" habitat, being very distinctive from the well-maintained plantation about 800 m away (Fig. 3). Although the cacao trees in both habitats are about the same age, the "cacao forest" habitat is heavily-shaded due to the presence of a well-developed canopy of forest trees (Fig. 3). The canopy of the "plantation" habitat is broken and uneven (Fig. 3).

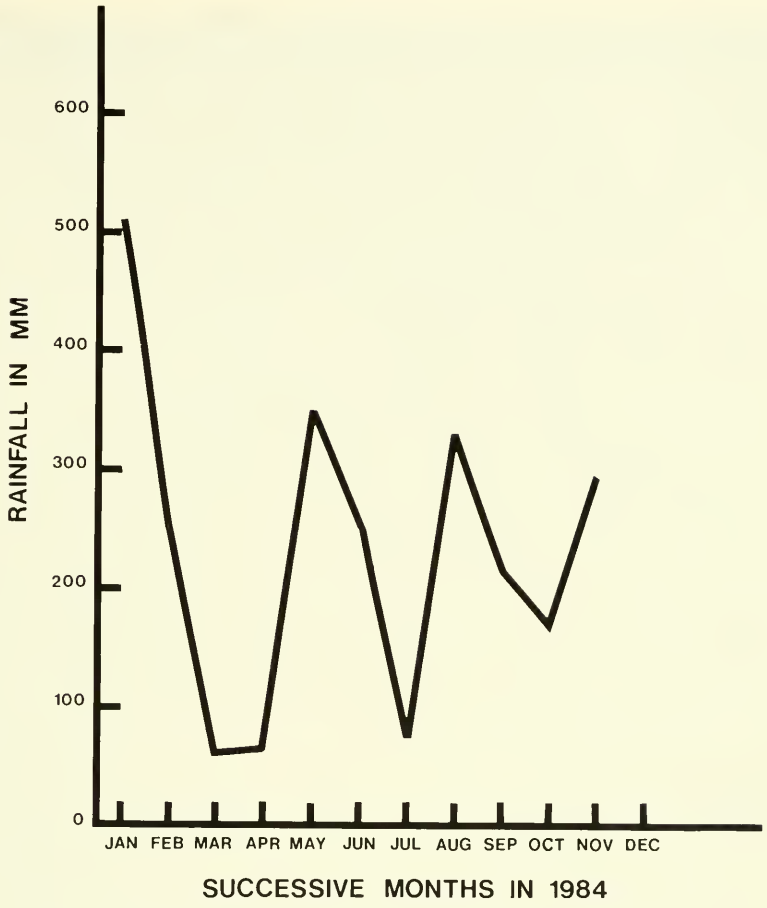

Fig. 2. Monthly rainfall pattern for "Finca Experimental La Lola" near Siquirres, Costa Rica, during the 1984 study period. Data courtesy of C.A.T.I.E. in Turrialba, Costa Rica.

Ground substrates were randomly distributed in the two cacao habitats as follows: five piles of rotting banana trunk slices (about 25 pieces or disks per pile); five piles of rotting pod husks, split-lengthwise, and with 30–40 husk-halves per pile; five 1 × 1 m wooden frames filled with rotting cacao leaves. The banana trunk slices, pod husks, and leaf litter were distributed around a total of fifteen tagged cacao trees in each habitat, using a random-numbers table to assign them within a larger pool of tagged trees. For each of the three censuses (March, August, and November 1984), these substrate treatments were replaced usually about two months prior to a census. A census consisted of sampling a total of 60 banana trunk slices, 75 pod husks, and 350 leaves (selecting those matted together) from each of the two habitats, and taking about the same number of items from each of the five replicates/treatment within each habitat. At the last of three censuses, I also sampled 30 arboreal rotten cacao pods from each habitat. Substrate materials were collected in large plastic bags and their contents examined at the La Lola field station.

The La Lola experimental study allowed a comparison not only of the ant

Fig. 3. La Lola cacao habitats studied. Top: "cacao forest" habitat on the property of Amos Barker. Note heavy shade and dense vegetation. Below: "Section 25" well-maintained cacao "plantation" habitat on La Lola property. Matina cacao trees are found in both habitats.

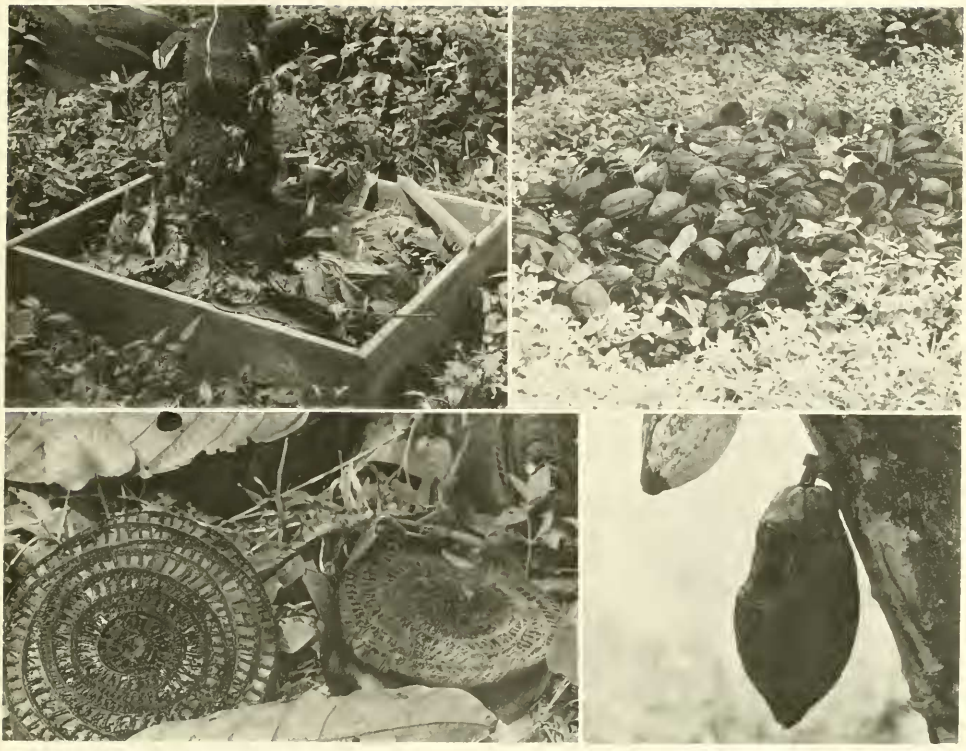

Fig. 4. Nesting substrates studied. Counterclockwise, beginning in upper left picture: wooden frame filled with cacao leaf litter; rotting trunk slices of banana trees; arboreal rotting cacao pod; pile of rotting cacao pod husks (halves).

faunas of two very different cacao habitats at the same locality, but also for microhabitat differences in terms of ant species and abundance patterns among substrates (Fig. 4). These data, in turn were compared with the arboreal pod ant data from the La Tigra locality, about 40 km to the north.

Ant voucher specimens from both studies were identified by Roy R. Snelling (Los Angeles County Museum of Natural History), and specimens are deposited both in the Los Angeles County Museum and the Milwaukee Public Museum insect collections.

Results

La Tigra arboreal cacao pods.—Although 1–3 pods out of 40 at each census contained termite colonies and no ants, by far most soft, well-rotten pods supported ant colonies, generally one species per pod. With the exception of the final census (November 1984), overall ant "occupancy" levels, for all pods on each census, ranged high, namely from about 30 to 90% (Table 1). For the first three censuses, four genera and species were found in the samples, and 60% of the ant "biomass" for the entire study (29,675 ants counted) were also found at these census periods. With the exception of the final census, *Crematogaster limata palans* Forel dominated all samples. The final pod census must be viewed an

Table 1. The distribution and approximate abundance of ant colonies in arboreal rotten *Theobroma cacao* L. (Sterculiaceae) pods at "Finca La Tigra," near La Virgen, Sarapiqui District, Costa Rica (N = 40 pods collected from the same area of cacao plantations for each of seven censuses).

Ant Species	Approximate Colony Size and Brood Over Census Periods											
	3–4 Dec. 1982 ("Late Rainy")			2–3 Mar. 1983 ("Dry")			7–8 Aug. 1983 ("Mid-rainy")			10–11 Nov. 1983 ("Late Rainy")		
	No. Nests**	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)
Camponotus abdominalis (Fabr.)	3	15–400	l, p							1	200	l, p
Crematogaster limata palans Forel	6	20–450	e, l, p	5	700–1000	e, l, p	9	15–350	l, p	13	20–500	e, l, p
Wasmannia auropunctata (Roger)	4	110–700	l, p				8	20–500	l, p	3	5–500	p
Paratrechina longicornis (Latr.)	3	100–300	l, p									
Solenopsis tenuis Mayr				6	500–1100	e, l, p						
Pheidole sp. 1				1	100	e						
Pheidole ares Forel							3	5–80	p			
Monomorium floricola (Jerdon)							2	1–30	—			
Solenopsis sp.							1	3	—			
Pachycondyla villosa (Fabr.)							2	1–6	p			
Camponotus planatus (Roger)										1	100	l, p
Crematogaster curvispinosa Mayr												
Tapinoma ramulorum Emery												
Pachycondyla crenata (Roger)												
P. carinulata (Roger)												
Neostruma metopia Brown												
% pods with ant colonies		16/40 = 40%			12/40 = 30%			25/40 = 62.5%			18/40 = 45.0%	
Total genera and additions ( )		4 (4)			4 (+2)			4 (+2)			1 (+0)	
Total species and additions ( )		4 (4)			4 (+2)			4 (+4)			1 (+1)	
Total "biomass"*		4/40			7150			6550			2678	

* Defined as the approximate total number of ants (adults and brood—e = eggs, l = larvae, p = pupae) observed.
** I assume that one nest equates with one colony.

Table 1. Continued.

Ant Species	Approximate Colony Size and Brood Over Census Periods								
	28–29 Feb. 1984 ("Dry")			3–4 Aug. 1984 ("Mid-rainy")			20 Nov. 1984 ("Late Rainy")		
	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)
Camponotus abdominalis (Fabr.)									
Crematogaster limata palans Forel	11	70–500	e, l, p	25	50–1000	e, l, p			
Wasmannia auropunctata (Roger)				4	5–100	e			
Paratrechina longicornis (Latr.)									
Solenopsis tenuis Mayr	5	50–300	l, p	5	50–500	p			
Pheidole sp. 1	1	15	l						
Pheidole ares Forel									
Monomorium floricola (Jerdon)									
Solenopsis sp.									
Pachycondyla villosa (Fabr.)									
Camponotus planatus (Roger)	2	5–20	–						
Crematogaster curvispinosa Mayr									
Tapinoma ramulorum Emery				1	30	e, l, p			
Pachycondyla crenata (Roger)				1	13	–			
P. carinulata (Roger)				1	1	–			
Neostruma metopia Brown							1	150	p
% pods with ant colonies		19/40 = 47.5%			37/40 = 92.5%			1/40 = 2.5%	
Total genera and additions ( )		1 (+0)			2 (+1)			1 (+1)	
Total species and additions ( )		1 (+1)			3 (+1)			1 (+1)	
Total "biomass"*		1456			7551			150	

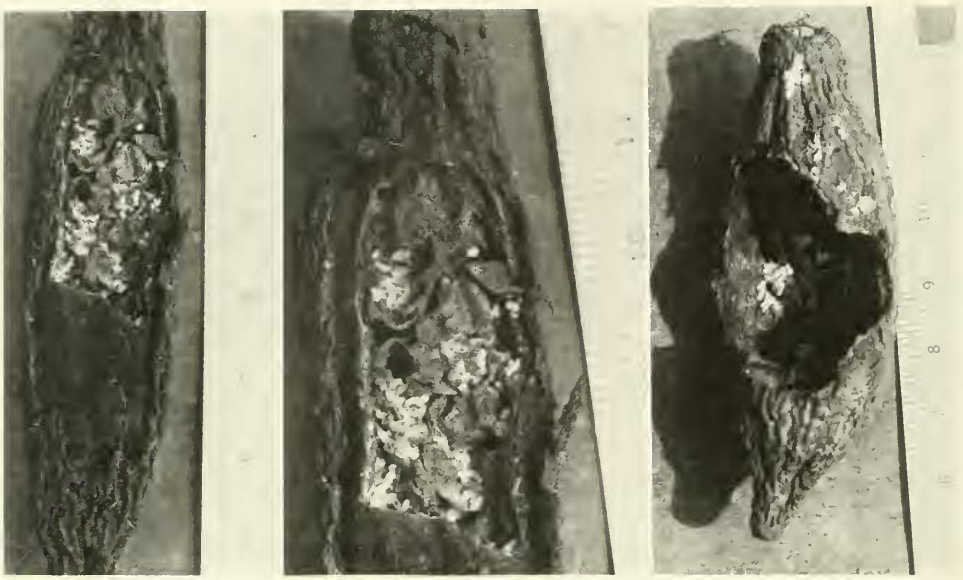

Fig. 5. Ant colonies (*Crematogaster limata palans* Forel) inside central (seed) cavities of arboreal rotting cacao pods at La Tigra. The pods have been broken open to show the colonies (with brood). Scale in mm.

anomaly, since almost all pods collected at this time were very hard and mummified due to the recent spread of the *Monilia* fungus pathogenic specifically to *Theobroma* and *Herrania* (Sterculiaceae) pods (e.g. Jorgenson, 1970). Such pods become extremely hard, precluding any colonization by insects. Ant colonies flourish inside moist. decaying pods on cacao trees, as evidenced by the majority of pods with ants also having brood (Fig. 5).

For both species number and ant biomass, I could not detect any definitive pattern between dry and rainy times of the year at La Tigra. Thus although the February 1984 census yielded the lowest ant biomass (with the exception of the November 1984 census), it also produced three species not previously collected. Furthermore, the March 1983 census, also a dry period, yielded more than five times the ant biomass as the later (February 1984) dry season census (Table 2). The observed total species richness of the arboreal pod ants at La Tigra was a product of successive censuses, as several additional genera and species were added by repeated censuses from the same cacao grove (Table 2).

Crematogaster limata palans Forel, *Wasmannia auropunctata* (Roger), *Paratrechina longicornis* (Latreille), and *Solenopsis tenuis* Mayr, were the most numerically-abundant ant species in my La Tigra samples, both in terms of colony size per census and their occurrence in successive censuses (Table 1). The relatively large (12 mm long body) ant *Camponotus abdominalis* (Fabricius) was also found within the wooden beams of the La Tigra field station. Pods with colonies of *C. abdominalis* were occasionally confined to clear plastic bags to determine when workers exited the nests: workers were not seen outside of the pods until 2000 hours (e.g. as seen on 2 March 1983).

In all cases only one ant species with brood was found inside a single cacao pod. One pod collected in August 1984 contained a four-celled nest of *Euglossa*

Table 2. Evidence for genera and species "replacement," and associated changes in ant "biomass" with successive censuses of arboreal, rotten cacao pods at "Finca La Tigra" in northeastern Costa Rica (for N = 40 pods examined per census).

Census mo/yr	Total Genera	Total Species	New Genera	New Species	Total Ant Numbers
Dec. 1982	4	4	—	—	4140
Mar. 1983	2	2	+2	+2	7150
Aug. 1983	4	4	+2	+4	6550
Nov. 1983	1	1	0	+1	2678
Feb. 1984	1	1	0	+1	1456
Aug. 1984	2	3	+1	+3	7551
Nov. 1984	1	1	+1	+1	150
Totals	—	—	10	16	29,675

bee species within the central (seed) cavity. This pod also contained a small colony of *C. limata palans* confined to the pod wall near the petiole. *Crematogaster limata palans* colonies were found both within the pod wall tissues and central cavity of pods.

Insects, including the larval and pupal stages of Diptera, particularly Ceratopogonidae and Cecidomyiidae, were occasionally found in pods with ants, but more frequently in pods unoccupied with ant colonies. Usually 1–4 larvae and/or pupae of the ceratopogonid *Forcipomyia cinctipes* group were found in pods with *C. limata* in particular. But larval abundance of this midge increased to 20–40 per pod in pods without *C. limata* and other ants. Likewise, 1–2 larvae of Cecidomyiidae were found in pods with *C. limata,* and higher numbers in pods without ants. Midge larvae and other insects, such as at least three species of Staphylinidae, were not found within ant colonies, but generally in other portions of the same pod. Virtually all pods with ants and other insects inside them were very soft and moist, and easy to crush with gentle pressure from the fingers. These pods also were not broken, i.e. they did not have holes. In *Theobroma cacao* L. the pods do not drop from the tree when mature.

Of all ants found in the La Tigra pod samples over all seven census dates combined, 70% were *C. limata.* Of the total 128 ant colonies found in the 280 pod-sample for all dates (45.17%), 69 of these, or 53.91%, were *C. limata palans.* No ant species was found in all seven censuses, but *C. limata palans* occurred in six. *Wasmannia auropunctata* ranked second most numerous, appearing in four censuses, followed by *Solenopsis tenuis* in three, and both *C. abdominalis* and *Pheidole* sp. 1 in two. All other thirteen ant species found in this survey occurred only once (i.e. were "rare"). The genera *Crematogaster, Solenopsis, Pheidole, Camponotus,* and *Pachycondyla* were each represented by two species in the La Tigra arboreal cacao pod censuses.

La Lola ground-nesting studies.—A total of 19 genera and 26 species of ants were found in the "cacao forest" adjacent to La Lola, while only 12 genera and 16 species were found in the "plantation" habitat at La Lola during the same period (Tables 3 and 4). All but two species found in the cacao plantation (*Pachycondyla impressa* (Roger) and *Odontomachus crythrocephalus* (Emery) were also found in the cacao forest habitat, considering all substrates and seasons examined (Tables 3 and 4). But the cacao forest had an additional 12 species not found at

Table 3. The distribution and approximate abundance of ants in various substrates in the "cacao forest" habitat at "Finca Experimental La Lola," near Siquirres, Limon Province, Costa Rica.

		Numbers of Individuals (Colonies) Distributed in Various Substrates		
		Banana Trunk Slices (N = 60/census)		
Census Date	Ant Species	No. Nests**	Range in Colony Size	Brood (?)
7–10 March 1984 ("dry")	*Smithistruma alberti* (Forel)	6	20–150	p
	Cyphomyrmex minutus Mayr	1	100	l, p
	Strumigenys lanuginosa Wheeler	1	75	l, p
	Pachycondyla stigma (Fabricius)	1	2	—
	Solenopsis sp. 2	2	50–100	l, p
	Solenopsis sp. 1	2	5–100	l, p
	Solenopsis sp.	2	10–60	l, p
	Oligomyrmex sp.	1	1	—
	Gnamptogenys striatula (Emery) group	2	40–150	p
	Gnamptogenys striatula (Emery) group	1	30	—
	Hypoponera nitidula (Emery)	1	40	p
	Cyphomyrmex salvini Forel			
	Megalomyrmex silvestrii Wheeler			
	Cyphomyrmex minutus Mayr			
	Paratrechina sp.			
	Brachymyrmex sp.			
Total genera 12				
Total species 16				
8–12 Aug. 1984 ("mid-rainy")	*Strumigenys rogeri* Emery	4	20–75	e, p
	S. elongata Roger	1	20	p
	Prionopelta amabilis Borgmeier	1	10	—
	Solenopsis sp. 2	13	25–100	e, l, p
	Smithistruma alberti (Forel)	4	50–100	e, l, p
	Wasmannia auropunctata (Roger)	2	5–20	p
	Hypoponera sp. (*opacior* group)	1	8	l
	Gnamptogenys striatula (Emery) group	7	25–150	l, p, alates
	Ectatomma ruidum Roger	1	5	—
	Hypoponera nitidula (Emery)			
	Cyphomyrmex salvini Forel			
	Cyphomyrmex minutus Mayr			
	Pheidole sp. 15			
	Paratrechina sp.			
	Odontomachus minutus Emery			
	Thaumotomyrmex paludis Weber			
Total genera 14				
Total species 16				
12–16 Nov. 1984 ("late rainy")	*Solenopsis* sp. 2	6	50–150	l, p, alates
	Gnamptogenys striatula (Emery) group	4	30–150	p
	Neostruma zeteki Brown	4	30–60	e, l, p
	Pheidole sp. 2	1	250	p, alates
	Strumigenys elongata (Roger)	1	20	l
	Prionopelta amabilis Borgmeier	4	10–100	e, p
	Smithistruma alberti (Forel)	5	70–150	e, l, p
	Hypoponera nitidula (Emery)	2	70–150	p
	Solenopsis tenuis Mayr			
	Cyphomyrmex minutus Mayr			
	Pheidole sp. 4			
Total genera 9				
Total species 11				
Overall distinct genera 19				
Overall distinct species 26				

Table 3. Extended.

Numbers of Individuals (Colonies) Distributed in Various Substrates								
Cacao Pod Husks (N = 75/census)			Leaf Litter (N = 350/census)			Arboreal Rot. Pods (N = 30/census)		
No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)
			1	20	p			
			6	10–100	p			
1	50	p	5	5–50	p			
1	10	p						
3	150–300	l, p					No Data	
1	150	p						
			2	20–30	p			
			1	40	p			
			1	40	p			
2	20–50	e	1	1	—			
2	20–40	e	7	50	e		No Data	
			5	20–30	e			
12	15–100	p, alates	6	35–100	e, p			
1	20	—						
2	15–50	p						
			1	30	e			
			1	50	e			
			1	30	e			
			1	1	—			
1	1	—						
2	30–70	l, p	5	50–60	l, p			
			1	80	l, p			
1	40	p						
1	25	p						
1	30	p				5	200–800	l, p
			1	10	l, alates			
						1	100	p

Table 4. The distribution and approximate abundance of ants in various substrates in the "cacao plantation" habitat at "Finca Experimental La Lola," near Siquirres, Limon Province, Costa Rica.

		Numbers of Individuals (Colonies) Distributed in Various Substrates		
		Banana Trunk Slices (N = 60/census)		
Census Date	Ant Species	No. Nests**	Range in Colony Size	Brood (?)
7–10 March 1984 ("dry")	*Solenopsis tenuis* Mayr	1	50	p
	Solenopsis sp. 2	1	30	l, p
	Gnamptogenys striatula (Emery) group	1	30	p
	Hypoponera nitidula (Emery)	1	3	—
	Oligomyrmex sp.	8	20–100	l, p
	Paratrechina sp.	1	3	—
	Pheidole sp. 15			
	Odontomachus minutus Emery			
	Pachycondyla impressa (Roger)			
Total genera 8				
Total species 9				
8–12 Aug. 1984 ("mid-rainy")	*Gnamptogenys striatula* (Emery) group	4	5–50	e
	Strumigenys rogeri Emery	2	50–100	e, p
	Wasmannia auropunctata (Roger)	1	50	e
	Solenopsis sp. 2	10	50–100	e
	Smithistruma alberti (Forel)	1	80	p
	Prionopelta amabilis Borgmeier			
	Pheidole sp.			
	Odontomachus erythrocephalus Emery			
	Paratrechina sp.			
Total genera 9				
Total species 9				
12–16 Nov. 1984 ("late rainy")	*Solenopsis* sp. 2	5	25–80	l, p
	Solenopsis sp. 1	1	150	l, p
	Gnamptogenys striatula (Emery) group	2	12–25	l, p, alates
	Smithistruma alberti (Forel)			
	Wasmannia auropunctata (Roger)			
	Paratrechina sp.			
	Hypoponera nitidula (Emery)			
Total genera 6				
Total species 7				
Overall distinct genera 12				
Overall distinct species 16				

all in the plantation. Within the cacao forest, the habitat with the most diverse ant fauna, the following ant species were found at all three censuses: *Solenopsis* sp. 2, *Smithistruma alberti* (Forel), *Cyphomyrmex minutus* Mayr, and *Gnamptogenys striatula* (Emery) group (Table 3). The highest occupancy level for the rotting banana trunk slices (2 pieces occupied) was seen in the cacao forest for *Solenopsis* sp. 2 as well as in the plantation (N = 16 pieces occupied). In the cacao forest, both *S. alberti* and *G. striatula* followed closely, with N = 15 and 13 pieces occupied, respectively. For the plantation, both *G. striatula* and *Oligomyrmex* followed closely, with N = 7 and 8 pieces of trunk slices occupied, respectively. In both habitats, *Solenopsis* had the most species, namely, four in the cacao forest

Table 4. Extended.

Numbers of Individuals (Colonies) Distributed in Various Substrates								
Cacao Pod Husks (N = 75/census)			Leaf Litter (N = 350/census)			Arboreal Rot. Pods (N = 30/census)		
No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)
1	50	p						
1	20	l, p						
			5	40–60	p		No Data	
			1	200	p, alate			
			1	1	—			
			1	1	—			
2	50	p						
1	50	e						
			1	8	—			
			5	30–60	e, l, p			
1	100	e					No Data	
1	100	e						
1	20	e, l						
1	5	p						
			3	25–200	e, l, p			
2	400	l, p	3	30–50	p			
1	400	l, p						
3	50–200	l, p						
2	200–300	l, p	2	20–100	l, p			
			1	1	p (l)			

and three in the plantation. All other genera were represented by 1–2 species in the cacao forest, and by one species, with the one exception of *Pheidole* with two species, in the cacao plantation (Tables 3 and 4). There is a general indication of brood being present in both habitats for all three census periods (Tables 3 and 4).

For all census dates combined, the cacao forest habitat has both the highest number of species and ant biomass as compared to the nearby plantation, and much of the ant fauna is accounted for by the rotting banana trunk slices (Table 5). For both banana trunk slices and cacao pod husks, the occupancy levels in the cacao forest were almost twice those of the plantation (Table 5). The ground leaf litter tended to have the lowest ant biomass across all census dates. Occupancy

rate for all substrate-types tends to be less than, or near, 10% across all census dates, but the highest occupancy level occurred at the mid-rainy season census in the cacao forest (Table 5). From the sample of 30 arboreal rotten cacao pods in each habitat in November, only a single pod in the cacao forest yielded an ant colony (*S. alberti,* approx. 100 ants with brood). Unlike the La Tigra census a few days later, none of these pods was hardened with the *Monilia* disease.

In terms of both species number and biomass, it is clearly the banana trunk slice "microhabitat" that supports the largest component of both the forest and plantation habitat and faunas at the La Lola locality (Table 5).

Faunal "overlap" between La Tigra and La Lola.—Twelve of the sixteen species of ants found at La Tigra in arboreal rotten cacao pods were not found at La Lola, a faunistic non-overlap of 75.00%. Furthermore, several genera of ants in the La Tigra study were not found in the La Lola samples: *Camponotus, Crematogaster, Momorium,* and *Tapinoma.* Genera in common between the two localities include: *Pheidole, Pachycondyla, Solenopsis, Wasmannia, Paratrechina,* and *Neostruma.* Two species, *W. auropunctata* and *S. tenuis,* were found at both localities. Overall, the La Tigra pods harbored many more ant colonies than the banana trunk slices and husk-halves on the ground in both La Lola habitats.

Discussion

Within a habitat, the number of resident ant species, and their patterns of resource utilization, including nesting sites, is often determined by the diversity of microhabitats available (e.g. Carroll and Janzen, 1973; Cole, 1946; Haber et al., 1981; Kempf, 1972; Levings, 1983; Wilson, 1976a). My data suggest that for Costa Rican cacao habitats, the resident assemblages of ground-nesting ants is determined in part by the availability of different types of nesting substrates. There is a tendency to find different ant species when sampling a diversity of substrates (microhabitats) within a cacao habitat. Furthermore, the diversity of ground-nesting ant species tends to be greater in the "cacao forest" when compared to a well-maintained cacao plantation at the same locality. The prevailing complexity of the vegetation in an abandoned cacao habitat which is returning to forest, coupled with intense shade tending to provide very moist conditions throughout the year, may be key factors in promoting ant species richness in a cacao forest habitat in Costa Rica.

Several recent habitat studies of ants in Costa Rica suggest that a greater number of species occurs in forest habitats (e.g. Jeanne, 1979; Lieberman and Dock, 1982). A similar pattern may hold for other tropical regions as well (e.g. Cole, 1983; Leston, 1979; Levings, 1983; Wilson, 1976a). But Young (1983) found a greater number of ant species within the La Tigra cacao plantation than in an adjacent strip of mixed primary and secondary tropical rain forest, a result in direct contrast with the data presented here for La Lola. This difference may be explained, at least in part, by the differences in the cacao plantation habitats between La Tigra and La Lola. The La Tigra cacao plantation is considerably younger than La Lola, and it is characterized by a natural canopy of forest trees left behind when the understory was cleared for planting cacao trees. Furthermore, La Tigra has a brush layer of diverse herbaceous species, in direct contrast with the relatively uniform grass cover in the "Section 25" cacao grove at La Lola. Cacao plantation age,

combined with the degree to which natural vegetation occurs in the plantation, may determine in large part the ant assemblages of the plantation. A vegetationally more diverse cacao habitat may provide a greater range of resources for ant species. Presumably the cacao forest adjacent to La Lola is more resource-rich for ants, and perhaps other insects, than the La Lola plantation itself, a pattern suggested by my data. Such a contention would also support the unusual case of cacao habitats sometimes having diverse ant faunas (Young, 1983).

A greater number of ant species was found in the ground-substrate censuses at La Lola than in the rotten arboreal cacao pods at La Tigra. This is not an unexpected finding, given the greater heterogeneity and larger sample sizes of the La Lola substrates compared to the La Tigra study. What is interesting, however, is the apparently high degree of species non-overlap between the La Tigra arboreal surveys and the La Lola ground surveys. To what degree such a difference is due to unexplained differences between the two localities or due to the nature of the microhabitat stratification (i.e. arboreal versus ground-nesting/foraging) cannot be deduced from my study. Yet some ant species in the tropics are largely arboreal nesters (e.g. Hilje, 1980; Huxley, 1980; Levieux, 1975; Levieux and Louis, 1975; Swain, 1980; Wilson, 1971 and many included references). Thus it would not be surprising to discover that my observed differences between La Tigra and La Lola were due largely to an effect of vertical stratification within the cacao habitat. At La Lola, up to about 10% of the insects found on cacao foliage are ants (Andrews, 1979). Arboreally-nesting ant species in cacao may also actively forage in the cacao foliage, as suggested by ant studies in the tropics (e.g. Carroll and Janzen, 1973; Wilson, 1976b; Swain, 1980).

Several of the ant genera found ground-nesting at La Lola are well known for nesting in a range of ground-level microhabitats (e.g. Mann, 1920; Wheeler, 1906, 1911, 1913; Wheeler and Mann, 1914), even though some genera and species are found both terrestrially and arboreally for nesting sites (e.g. Kempf, 1972; Wilson, 1971). The presence of *Camponotus planatus* (Roger) in arboreal rotten cacao pods at La Tigra complements earlier observations of this ant being a stem dweller in the Guanacaste Province of Costa Rica (Carroll and Janzen, 1973). O'Dowd (1979) found that *Solenopsis* was common on ground-level honey baits while *Crematogaster* was common at arboreal honey baits. My data clearly shows a similar pattern for nesting differences between these two genera. Similarly, *Crematogaster limata,* by far the most abundant ant species discovered nesting arboreally in cacao pods at La Tigra in my study, commonly forages in vegetation in Costa Rica (Jeanne, 1979). But *Solenopsis tenuis,* nesting both arboreally and terrestrially in cacao habitats in my study, also forages primarily in vegetation in Costa Rica (Jeanne, 1979). Robert Jeanne (1979) also found that *Solenopsis* and *Pheidole* foraged primarily on the ground. Together with observations of yet other species occurring both arboreally and terrestrially in the tropics (e.g. Kempf, 1972; Wheeler and Mann, 1914), such observations suggest that some ant species are resource "generalists" in terms of utilizing both terrestrial and arboreal resources, while others are much more restricted in this sense.

My observations of a few ant species "dominating" within a habitat, in terms of colony size and the frequency of occupancy among substrate (nesting) parcels, is not unusual for tropical agricultural habitats (e.g. Adams et al., 1981; Leston, 1973, 1978; Saks and Carroll, 1980; Samways, 1981, 1983). Even though lowland

Table 5. Effects of habitat-type ("cacao forest"; "cacao plantation") and season ("dry"; "mid-rainy"; "late rainy") on the overall distribution and abundance of ant species in various substrates at "Finca Experimental La Lola," near Siquirres, Limon Province, Costa Rica.

	Distribution of Individuals ("Biomass") and Species Among Habitats and "Seasons"							
	7–10 March 1984 ("Dry")				8–12 August 1984 ("Mid-rainy")			
	Cacao Forest		Cacao Plantation		Cacao Forest		Cacao Plantation	
Substrate Type and % Occupancy	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species
Banana trunk slices (60 + 60)*	930	11	375	6	1436	9	908	5
% Occupied	20/60 = 33.33%		13/60 = 21.67%		34/60 = 56.67%		18/60 = 30.00%	
Pod husks (75 + 75)	850	4	70	2	665	6	325	6
% Occupied	6/75 = 8.00%		2/75 = 2.67%		19/75 = 25.33%		7/75 = 9.33%	
Leaf litter (350 + 350)	548	6	510	4	1022	8	543	3
% Occupied	15/350 = 4.28%		8/350 = 2.29%		19/350 = 5.43%		9/350 = 2.57%	
Arbor. rot. pods (35 + 35)	No Data		No Data		No Data		No Data	
% Occupied								
Diseased pods on ground (35 + 35)	No Data		No Data		No Data		No Data	
% Occupied								
Totals across substrates	2328		955		3123		1776	
Overall % occupancy	41/485 = 8.45%		23/485 = 4.74%		72/485 = 14.85%		34/485 = 7.01%	

* Numbers in parentheses refer to the number of substrate pieces sampled in each of the two cacao habitats.

Table 5. Continued.

Substrate Type and % Occupancy	Distribution of Individuals ("Biomass") and Species among Habitats and "Seasons"									
	12–16 November 1984 ("Late Rainy")				Total Cacao Forest		Total Cacao Plantation		Overall Total Combined Habitats	
	Cacao Forest		Cacao Plantation							
	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species
Banana trunk slices (60 + 60)*	2265	8	477	3	4631		1760		6391	
% Occupied	27/60 = 45.00%		8/60 = 13.33%		81/180 = 45.00%		39/180 = 21.67%		120/360 = 33.33%	
Pod husks (75 + 75)	195	4	2050	4	1710		2445		4155	
% Occupied	5/75 = 6.67%		8/75 = 10.67%		30/225 = 13.33%		17/285 = 7.56%		47/450 = 10.44%	
Leaf litter (350 + 350)	480	3	231	3	2050		1284		3334	
% Occupied	7/350 = 2.00%		6/350 = 1.71%		41/1050 = 3.90%		23/1050 = 2.19%		64/2100 = 3.05%	
Arbor. rot. pods (35 + 35)	3300	2	0	0	—		—		—	
% Occupied	6/35 = 17.14%		0.00%		—		—		—	
Diseased pods on ground (35 + 35)	0	0	100	1	—		—		—	
% Occupied	0.00%		1/35 = 2.85%		—		—		—	
Totals across substrates	6240		2858		8391		5489		13,880	
Overall % occupancy	45/485 = 9.28%		23/520 = 4.42%		152/1455 = 10.45%		79/1455 = 5.43%		231/2910 = 7.94%	

tropical rain forest sites are expected to be very rich in ant species (e.g. Ayre, 1977; Evans, 1982; Kempf, 1974, 1975; Levings, 1983; Levings and Franks, 1982) and for insects in general (e.g. Amendegnato and Descamps, 1980; Hanski, 1980) cacao and other lowland agricultural habitats tend to have less diverse ant faunas characterized by specific "assemblages" of species (e.g. Bigger, 1981; Jackson, 1984; Leston, 1973, 1978, 1979). Genera such as *Crematogaster, Pheidole,* and *Solenopsis* dominate such assemblages in cacao and other tropical crop habitats throughout the world (e.g. Samways, 1981, 1983).

There is some evidence that ants prefer nesting in the most shaded patches within a cacao habitat (e.g. Ackonor, 1981, 1983; Leston, 1973). Both ground-level and arboreally-active insects in lowland tropical forests may exhibit fluctuations in both abundance and overall species richness in direct response to tropical seasonality (e.g. Baker, 1976; Fisk, 1982; Levings, 1983). Ant species in cacao habitats may preferentially seek well-shaded nesting microhabitats as a means to "buffer" the impact of the tropical dry season, even in localities where seasonal cycles of rainfall are less pronounced. My data did not reveal any definitive patterns of seasonal changes in the structure of ant assemblages in cacao habitats, possibly because my censuses were too widely-scattered, and my sample sizes at each census, relatively small. The maintenance of a shade cover throughout much of the year in the La Lola cacao forest may be a major influence upon the overall observed high species richness of ants found there. Naturally-rotting arboreal cacao pods provide a very moist nesting microhabitat off the ground. Healthy pods, gouged out by vertebrates seeking the sweet-tasting pulp of cacao seeds, very seldom become colonized by ants once they rot. Intact, unbroken pods are frequently colonized by a diverse ant fauna, as shown here. Furthermore, halved pod husks on the ground are not as suitable as nesting microhabitats as are rotting banana trunk slices. In terms of overall attractiveness as nesting sites for diverse assemblages of ant species, the ground-level banana trunk slice replaces the intact rotted arboreal cacao pod as a frequently colonized resource in cacao habitats in Costa Rica. Such observations suggest that microhabitat "attractiveness" for tropical ant nesting is governed largely by physical parameters (i.e. moisture-retention and darkness) rather than intrinsic chemical attractiveness of well-rotted plant tissues (i.e. cacao pod walls versus banana trunk slices).

About 20% of the forest foliage insects in a tropical forest habitat, in the understory, can be ants, contrasted with about half this frequency for cacao habitats (Andrews, 1979). In some instances, however, open canopy habitats may promote species-rich ant assemblages in the tropics (e.g. Jeanne, 1979 and see also Thompson, 1981 for general discussion).

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NOTE

The Hickory Aphid, *Protopterocallis fumipennella* (Fitch) and its Junior Synonym, *P. canadensis* Richards, New Synonymy (Homoptera: Aphididae)

The identity of *Aphis fumipennella* Fitch has always been problematical. Bissell (1932. Ann. Entomol. Soc. Am. 25: 730–735) thought the type specimen too broken for full identification. Smith and Parron (1978. North Carolina Agric. Exp. Sta. Tech. Bull. 255: 1–428) quoted from my correspondence and listed it as "*Protopterocallis* ? *fumipennella* (Fitch) nomen dubium," adding 12 state records, evidently based on the determinations of *Myzocallis fumipennellus* (Fitch), a misidentification for the black pecan aphid. I believe these entries are largely in error. Knowlton (1983. Utah Agric. Exp. Sta. Bull. 509: 1–199) listed *P. fumipennella* on pecan at St. George, Utah; this is definitely an error for *Melanocallis caryaefoliae* (Davis).

In my earlier report on the type specimen (Bissell, 1932. Ibid.) I included the primary sensorium with the unguis in my measurements; however, when included with the base, antennal segment 6 is 0.143 plus 0.045, that is, base three times as long as unguis. Another character in common between *fumipennella* and *canadensis* (below) is the presence of three small tubercles on the posterior margin of the head, dorsally.

Richards (1965. Entomol. Soc. Can. Mem. 44: 1–149) erected *Protopterocallis* for a new species, *P. canadensis* Richards. Bissell (1978. Maryland Agric. Exp. Sta. Misc. Publ. 911: 1–78) gave additional information on the genus. Since that time I have reexamined the type of *fumipennella* as well as additional specimens from the type locality, Salem, New York and cannot find morphological differences between *fumipennella* and *canadensis*. I therefore declare them synonyms. This species has been most common on *Carya cordiformis* Wang (K. Koch) but has also been taken on *C. glabra* (Mill.) Sweet, *C. ovata* (Mill.) K. Koch and *C. tomentosa* (Poir.) Nutt., but not on pecan, *C. illinoensis* (Wang.) K. Koch.

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